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## NOTE

# A Novel Mechanism for a Survival Advantage of Vigilant Individuals in Groups

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Online enhancement: appendix.

**ABSTRACT:** In many animal species, vigilance is crucial for avoiding predation. In groups, however, nonvigilant individuals could benefit from the vigilance of others without any of the associated costs. In an evolutionary sense, such exploitation may be compensated if vigilant individuals have a survival advantage. The novelty in our model is that the probability to detect a predator is “distance dependent.” We show that even if nonvigilant individuals benefit fully from information produced by vigilant individuals, vigilant individuals nevertheless enjoy a survival advantage. This happens because detection of predators is more likely when vigilant individuals happen to be targets of predation. We expect this distance-dependent mechanism to be compatible with previously reported mechanisms.

**Keywords:** vigilance, group foraging, survival advantage, distance-dependent production, predation.

## Introduction

Antipredator vigilance is crucial for survival in many group-living animals. However, if information from vigilant individuals is immediately and perfectly shared with all other individuals in the group, then nonvigilant freeloaders might benefit from the vigilance effort of others without any of the associated costs, such as foraging time (McNamara and Houston 1992). Such a cooperative dilemma could undermine the maintenance of vigilance in groups. One solution to the problem of freeloaders is a survival advantage of vigilant individuals relative to nonvigilant ones. In evolutionary models, such a survival advantage can increase the levels of vigilance in groups (McNamara and Houston 1992; Beauchamp and Ruxton 2003; Sirot and Touzalin 2009).

Mechanisms generating a survival advantage of vigilant individuals should cause one's own vigilance to be more

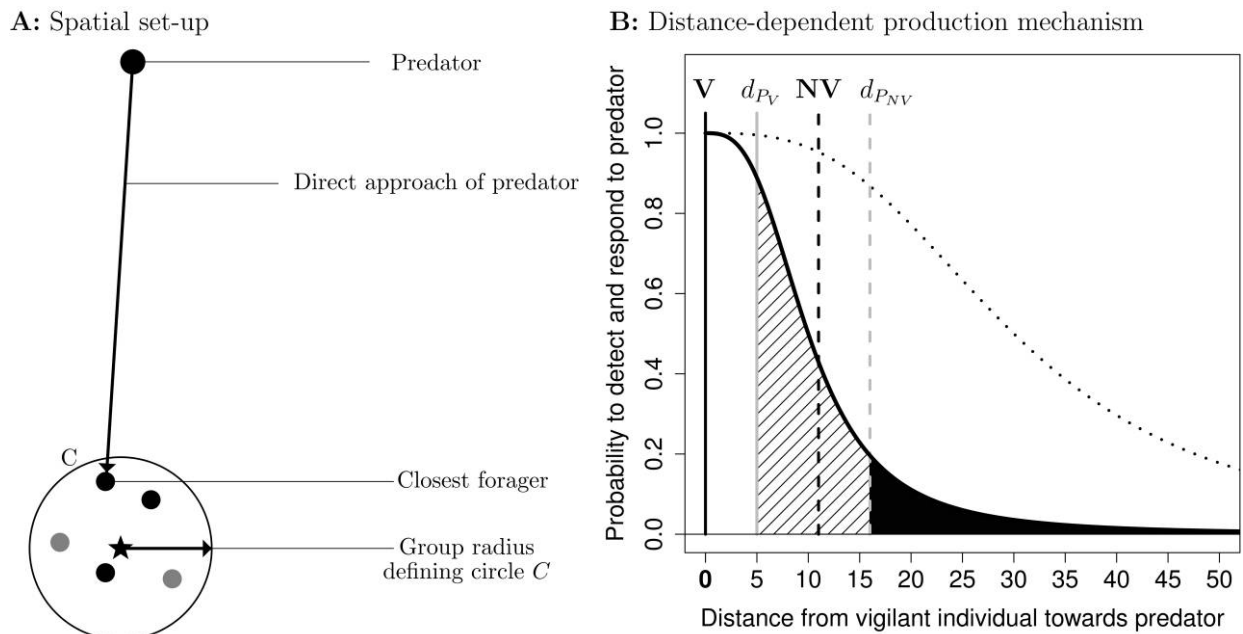
effective for oneself than for others. The two theoretical mechanisms that have been considered are (i) “faster response,” where the vigilant individuals that detect a predator will be able to respond first (Bednekoff and Lima 1998)—if the predator can alter its target late in an attack or chooses a target at the last moment, an individual with a high level of vigilance may actually increase the rate of predation of less vigilant individuals via a “pass-along” effect (Bednekoff and Lima 1998)—and (ii) “distance-dependent transmission” of information, where the spatial separation of individuals reduces the likelihood that nonvigilant individuals notice the antipredator response of vigilant individuals (Proctor et al. 2003, 2006; Beauchamp 2007).

However, both the faster response and the distance-dependent transmission mechanisms focus on transmission of information and not its production, and they have been studied in models where the detection of predators is a fixed probability (Bednekoff and Lima 1998; Proctor et al. 2003, 2006; Beauchamp 2007). Yet if the probability of detecting and producing information about a predator attack depends on distance from the predator, then individuals that are farther away from a predator are less likely to produce information. Individuals that are closer to the predator should therefore rely on their own vigilance. Thus, even without constraints on information transmission within groups, vigilant individuals could still enjoy a survival advantage. This possibility has not been studied before.

Here, we propose a novel mechanism through which vigilant individuals can enjoy a survival advantage, which we refer to as “distance-dependent production” of information. We use a simulation model to study how distance-dependent detection of predators affects survival of vigilant and nonvigilant foragers and elucidate whether a distance-dependent production mechanism can generate a survival advantage of vigilant foragers even when the transmission of information produced by vigilant individuals is immediate and perfect.

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**Figure 1:** The model. *A*, Setup at the beginning of an attack. The predator is 150 distance units from the group and targets the closest forager. Foragers are positioned randomly about the center (star) of a circle *C* with a given radius (filled circle). *B*, Distance-dependent production mechanism. The solid curve shows the distance-dependent decline of the probability of detecting and responding to the predator by a vigilant individual *V* (eq. [1]), where  $d_p$  is the critical distance at which a forager can be caught by the predator ( $=5$  m), and  $\alpha = 1$ ,  $h = 10$ , and  $N = 3$  (for comparison: dotted curve, where  $h = 30$ ). For *V*, the probability of escaping the predator is proportional to the area under the curve from  $d_{P_V}$  onward (dark and striped area combined). For nonvigilant individual *NV* (closer to the predator), the probability of escaping the predator is proportional to the dark area. The striped area represents the survival advantage of the vigilant forager.

### Model and Analysis

We make five assumptions: (i) a predator is initially far away from a group of foragers and targets the closest forager; (ii) a targeted forager must respond to a predator (e.g., flee) before the predator is within a critical distance  $d_p$  from the forager, otherwise the predator attacks and catches the forager while nontargeted foragers escape; (iii) if a forager responds to and escapes from a predator, other foragers automatically detect this response and also escape (perfect information transmission); (iv) a forager can detect the predator only when it is vigilant, and it is vigilant with probability  $p_v$  per time unit (when we refer to “detection” this also implies “response,” since in our model there is no distinction between the two); and (v) if a forager is vigilant, the probability  $p_R$  of a forager to detect and respond to a predator declines with distance  $d$  to the predator, as follows:

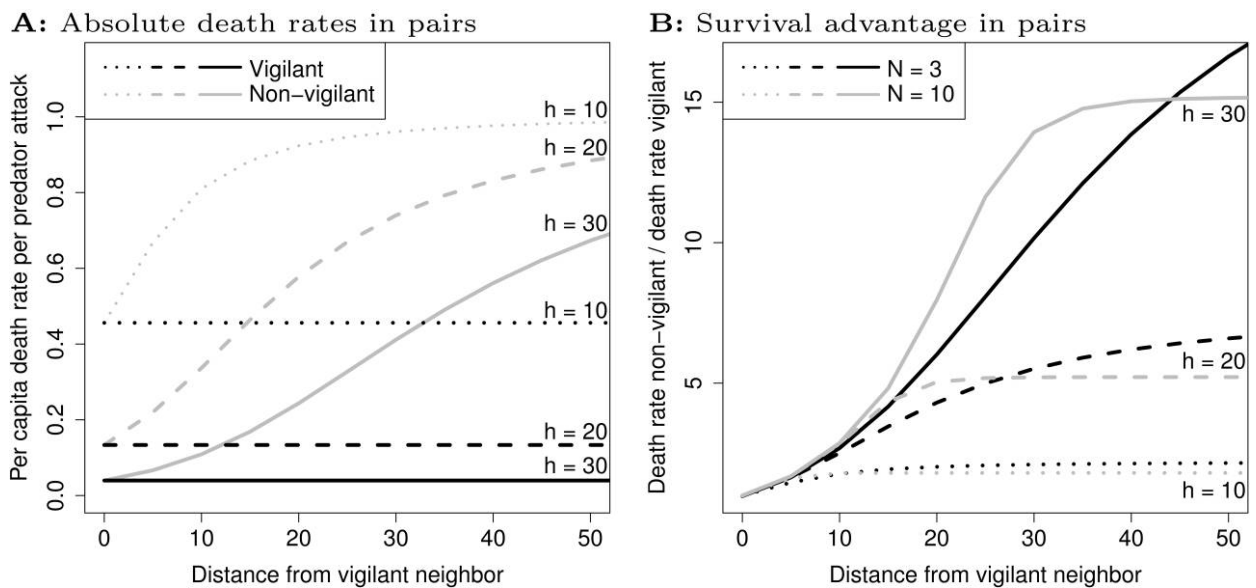
$$p_R = \alpha \left( \frac{h^N}{d^N + h^N} \right), \quad (1)$$

where  $N$  determines how steeply predator detection decreases with distance  $d$  to the predator,  $h$  is the distance

at which predator detection is half maximal, and  $\alpha$  sets the maximal detection rate. The detection function is shown in figure 1B (solid curve:  $h = 10$ ; dotted curve:  $h = 30$ ). The parameters of equation (1) will vary across species and contexts. For instance, habitats with limited visibility should correspond to low values for  $h$  and high values for  $N$ . The exact form of equation (1) does not have much importance. In the appendix (section A; appendix available online), we show that our findings are robust to changes in the functional form of the detection function.

We determine the impact of distance-dependent production on a survival advantage of vigilant foragers by running simulations in a spatially explicit model. We first measure predation rates in pairs of foragers, of which one is vigilant ( $p_v = 0.1$ ) and the other is nonvigilant ( $p_v = 0$ ). For each attack, a predator is initialized at 150 distance units from the pair, and the distance between the predator and its target decline with 1 distance unit per time unit. We then vary the distance between the two foragers.

To generalize our results, we repeat simulations with groups of 5, 10, and 20 foragers, where foragers are placed



**Figure 2:** Advantage of vigilant individuals in pairs as a function of distance between a nonvigilant target and a vigilant neighbor (distance between NV and V in fig. 1). *A*, Death rates of a nonvigilant target of predation (gray) for different levels of attenuation of predator detection rates with distance from the predator:  $h = 10$  (dotted),  $h = 20$  (dashed), and  $h = 30$  (solid). Black: reference point when both foragers are at exactly the same location and both experience the full benefit of vigilance. *B*, Survival advantage of a vigilant forager: nonvigilant death rate divided by vigilant death rate. Gray:  $N = 10$ ; black:  $N = 3$ ; dotted:  $h = 10$ ; dashed:  $h = 20$ ; solid:  $h = 30$ . Other parameters:  $\alpha = 1.0$ ,  $N = 3$ ,  $d_p = 5$ ,  $p_v = 0.1$ ,  $p_M = 0$ . Death rates were measured as the proportion of individuals caught over  $10^6$  attacks (every 5 distance units).

at a random location drawn from a uniform distribution within a circle  $C$  (fig. 1A) and any position within the circle is equally likely. We vary the proportion of vigilant individuals in groups in the range 0.0–1.0 at intervals of 0.2. We study the effect of interindividual distance by varying the radius of circle  $C$ . Since the targeting of foragers at the periphery of the group is important, we also vary the rate at which the predator changes its target by incorporating movement of foragers. A forager is repositioned with probability  $p_M$  per time unit, where its new location is randomly drawn from a uniform distribution within circle  $C$ . For all settings we simulate  $10^6$  predator attacks. The model is available online at <https://bitbucket.org/dvanderpost/vigilance-advantage>.

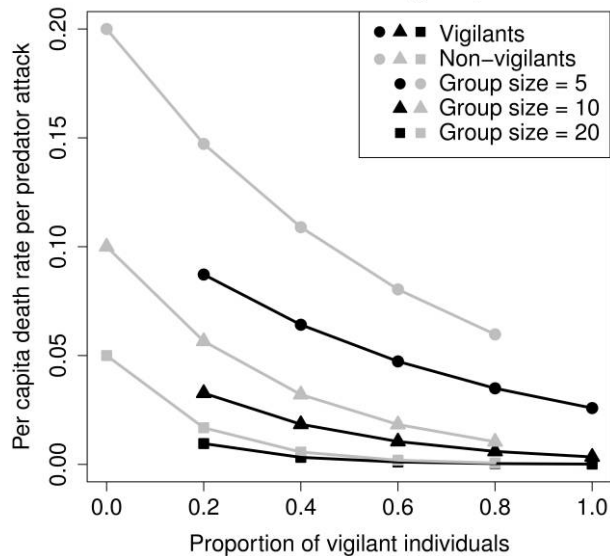
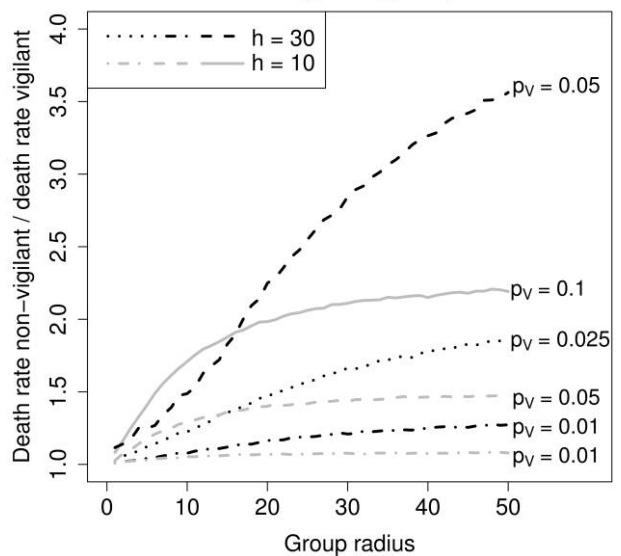
## Results

We illustrate the distance-dependent production mechanism for a survival advantage of vigilant individuals in figure 1B. A vigilant individual V enjoys the maximal probability to detect and respond to a predator on the basis of its own vigilance, which is proportional to the area under the curve from  $d_{p_v}$  onward (striped and dark area combined). In contrast, a nonvigilant individual NV relies on the vigilance of its vigilant neighbor V. If its vigilant

neighbor is farther away from the predator than the nonvigilant individual itself (as in fig. 1B), then to avoid predation the predator must be detected (by its vigilant neighbor) over a shorter period of time, and during this time the predator is also relatively far away from the vigilant neighbor (dark area). The probability of escaping the predator is therefore reduced by a factor proportional to the striped area, which represents the survival advantage of the vigilant forager.

In figure 2A we show for pairs of foragers how the death rate of a nonvigilant target (gray curves) increases with distance from a vigilant neighbor, where black lines show death rates of the vigilant neighbor. We compare three levels of difficulty of detecting the predator by varying half-maximum values of equation (1) (dotted:  $h = 10$ ; dashed:  $h = 20$ ; solid:  $h = 30$ ), where larger values correspond to slower attenuation of detection rates with distance from the predator (compare solid and dotted curves in fig. 1B). With slow attenuation of detection rates ( $h = 30$ ), overall death rates are relatively low (solid black line). In addition, death rates of nonvigilant foragers increase more slowly with distance between the pairs (solid gray) than when detection rates attenuate faster (dotted and dashed gray).

To determine how the survival advantage of the vigilant

**A: Absolute death rates in groups****B: Survival advantage in groups**

**Figure 3:** Advantage of vigilance in groups. *A*, Death rates for vigilant (black) and nonvigilant (gray) foragers in groups with a radius of 10 for group sizes of 5, 10, and 20 (circles, triangles, and squares, respectively) and varying proportions of vigilant foragers. Parameters:  $\alpha = 1.0$ ,  $h = 10$ ,  $N = 3$ ,  $d_p = 5$ ,  $p_v = 0.1$ ,  $p_M = 0$ . *B*, Survival advantage (nonvigilant death rate divided by vigilant death rate) with increasing group radius for a group size of 5 and a proportion of vigilant foragers of 0.8. Black:  $h = 30$ ; gray:  $h = 10$ ; solid:  $p_v = 0.1$  (black not shown, since survival advantage values are too large); dashed:  $p_v = 0.05$ ; dotted:  $p_v = 0.025$  (gray not shown, since it mostly overlaps with black dotted-dashed); dotted-dashed:  $p_v = 0.01$ . Other parameters:  $\alpha = 1.0$ ,  $d_p = 5$ ,  $p_M = 0$ . Death rates were measured as the proportion of individuals caught over  $10^6$  attacks (every distance unit).

forager changes with distance for a given pair, we express the advantage as  $d_{NV}/d_V$ , where  $d_{NV}$  and  $d_V$  are the death rates of nonvigilant and vigilant foragers, respectively. Thus, a twofold increase in  $d_{NV}$  generates a twofold survival advantage for the vigilant forager (given that  $d_V$  is fixed), and it is maximal when  $d_{NV} = 1$ . In figure 2B, we show how the survival advantage appears as soon as the pair becomes separated (all curves) and increases fastest when predator detection rates attenuate most slowly with distance from the predator (solid curves). The pattern is qualitatively similar for different values of  $N$  (compare black to gray). When predator detection attenuates slowly with distance, the death rates of vigilant foragers are lower (fig. 2A, black lines). Hence, the maximal difference in death rates between vigilant and nonvigilant foragers ( $1 - d_V$ ) is greater, thus generating a greater maximal survival advantage for vigilant foragers ( $1/d_V$ ). As a result, although absolute death rates of nonvigilant foragers increase more slowly with distance when predator detection attenuates more slowly (fig. 2A), the survival advantage increases more rapidly (fig. 2B). The crossing of curves with different values of  $N$  (fig. 2B, black and gray curves of a given type) indicates that the survival advantage increases more rapidly but reaches a maximum earlier, when  $N$  is greater (gray lines). For larger  $N$ , high detection rates are increasingly

limited to small distances (less than  $h$ ), causing a more rapid initial increase in the survival advantage of the vigilant individual. However, a larger  $N$  causes a greater death rate ( $d_V$ ) of vigilant foragers and, hence, a lower maximum survival advantage ( $1/d_V$ ).

In groups of more than two individuals we observe the same patterns. First, death rates are greater for nonvigilant (gray) than for vigilant (black) individuals (fig. 3A). Second, the survival advantage of vigilant foragers increases as interindividual distances increase (fig. 3B, from left to right). Note that absolute death rates increase for both vigilant and nonvigilant foragers since they all end up farther from vigilant neighbors (see the appendix, section B). However, death rates increase faster for nonvigilant foragers, giving rise to a greater survival advantage. Third, the survival advantage increases more rapidly with distance when predator detection is more likely (fig. 3B, going from bottom to top curves). This third pattern is observed both with respect to increasing vigilance levels (from bottom to top for a given color) and with respect to a slower attenuation of detection rates with distance (from gray to black for dashed and dotted-dashed lines). In figure 3B, we show data from simulations with a group size of 5 and a proportion of vigilant foragers of 0.8. Other group sizes

and proportions give qualitatively similar results (see the appendix, sections C and D).

The other main effect of increasing group size is an overall reduction in death rates due to the “dilution” and “many-eyes” effects (fig. 3A). The many-eyes effect is apparent from the decline in death rate as the proportion of vigilant individuals increases (fig. 3A, from left to right). The dilution effect is apparent from the decline in death rate as group size increases, when the proportion of vigilant foragers is 0 (fig. 3A, from circles to triangles to squares). For groups with vigilant foragers (proportion  $\geq 0.2$ ), the dilution effect and the many-eyes effect interact.

Vigilance can become so effective that predation on vigilant foragers is no longer observed. In figure 3B, we therefore choose to show data from a group size of 5, where death rates are greatest, so that a larger range of vigilance rates ( $p_v$ ) can be shown. Results are qualitatively similar with larger group sizes, but the values of  $p_v$  at which predation is no longer observed are lower (see the appendix, section C). With respect to the ease of predator detection, we therefore observe two conditions for a survival advantage of vigilant foragers: (i) predator detection should be possible, otherwise there is no difference in death rate between vigilant and nonvigilant foragers, and (ii) predation on vigilant foragers should be possible, otherwise relatively large interindividual distances are required before the survival advantage for vigilant foragers arises (see the appendix, section B).

Since the survival advantage of vigilance depends on the difference in detecting the predator when targets of predation are either vigilant or nonvigilant, we consider the effect of changes in the constancy of targeting a specific prey. For this, we vary the rate with which individuals change their position in the group ( $p_M$ ) and find that the advantage of vigilant individuals declines as the probability to move increases (see the appendix, section E). This happens because a more well-mixed situation is generated when individuals move, such that vigilant and nonvigilant individuals end up benefiting more equally from vigilance in the group. Any difference between vigilant and nonvigilant individuals is then restricted to the time period between the last targeting and the actual attack by the predator. This interval is reduced as movement rates increase.

### Discussion

We have proposed a novel mechanism through which a survival advantage for vigilant individuals can arise: if targets of predation are on the periphery of groups and the probability of detecting predators declines with distance, then vigilance by a target is more likely to detect a predator than vigilance by another vigilant individual that is farther

away from the predator. Thus, vigilant individuals should rely on their own vigilance even when information about predators is shared equally among group members. This mechanism, based on distance-dependent production of information, could be an important factor contributing to variation in patterns of vigilance among animals and is robust to changes in the form of the detection function (see the appendix, section A).

Our analysis reveals that several conditions must be met for this mechanism to function. First, predators must target and catch peripheral individuals more often. Such an “edge effect” (Inglis and Lazarus 1981; Proctor et al. 2006) has been documented in a range of species (Krause and Ruxton 2002). In our model, the edge effect arises because we assume that predators approach groups from a distance and target the closest forager. This appears to be a reasonable starting assumption and is standard practice for spatial models (Hamilton 1971; Oboshi et al. 2002; Reluga and Viscido 2005; Kunz et al. 2006; Beauchamp 2007).

Second, detection and production of information about the predator must decline with distance from the predator. Such distance dependence has been demonstrated in experiments with birds (Lima and Bednekoff 1999; Tisdale and Fernandez-Juricic 2009) and is expected to be more extreme in smaller birds and mammals because visual acuity declines with body size (Kiltie 2000). In addition, it is important to consider that the motivation to respond to a predator also declines with distance (Fernandez-Juricic et al. 2002; Cooper and Frederick 2007). Thus, even if vigilant neighbors detect predators, if they are far away from the predator they may not respond with a sufficiently salient cue to inform nonvigilant foragers.

In the experiments with birds (Lima and Bednekoff 1999; Tisdale and Fernandez-Juricic 2009), detection rates attenuate relatively slowly with distance (e.g.,  $h \geq 30$ ). However, the probability of predator detection also depends on vigilance levels ( $p_v$ ). Important in this respect is the speed with which the predator approaches, which in our model is relatively slow (3.6 km/h, when scaled to 1 m/s). The experimental studies concern small birds detecting raptors (Lima and Bednekoff 1999; Tisdale and Fernandez-Juricic 2009), and raptors may attack at high speeds (more than 30 km/h). To interpret our model with respect to such speeds requires a rescaling of time units and, hence, rates such as  $p_v$ .

The third condition is that individuals must forage in groups that are spread out in space, which is true for all group foragers. The question is whether distances between foragers in groups are large enough compared with the distances at which predators are detected. In figure 3B, it can be seen, for all group radii, that when predator detection rates attenuate slowly ( $h = 30$ ), the survival advantage of vigilant foragers is greater than when detection

rates attenuate fast ( $h = 10$ ). This is true as long as (i) vigilance can reduce predation and (ii) predation is not completely prevented, which are the relevant conditions when considering a survival advantage of vigilant foragers.

The fourth condition is that individual positions should be sufficiently stable so that the predator need not change targets too often. In our simulations with movement (see the appendix, section E), we use a conservative assumption, namely that individuals move to a random position in the group circle. Such a randomization represents an extreme scenario for changes in positions because natural autocorrelations between positions are lost. We expect the impact of movement in animal groups to be less extreme, especially in those cases where predators approach groups rapidly, which reduces the number of movements during an attack. Nonetheless, the impact of movement should be further investigated in models with more natural movement of individuals, such as in models of self-organization (Oboshi et al. 2002; Wood and Ackland 2007; Hemelrijk and Hildenbrandt 2008; van der Post and Semmann 2011).

In principle, distance-dependent production should generate a survival advantage for vigilance if these four conditions hold. The magnitude of the advantage will depend on the interrelation between (i) group radius, (ii) predator speed, (iii) the detection function, (iv) vigilance rates, and (v) the rate with which the predator changes targets due to movements of foragers. If such parameters can be measured, implementing them in a simulation model like ours could give a rough initial expectation. Even so, the question of whether the absolute differences in death rate (which generate the survival advantage) are sufficient to be of importance for a particular species remains. The survival advantage is greater when vigilance is more effective but at the same time the absolute difference in death rates is smaller (see the appendix, sections B and C). The importance of absolute differences in death rates will depend on the life-history characteristics of a species.

To conclude, we point out that distance-dependent production of information does not exclude the faster response and distance-dependent transmission mechanisms. All three mechanisms could simultaneously contribute to a survival advantage of vigilant foragers, but it remains unknown to what extent. At present, there is evidence for both the faster response (Lima 1994; Hilton et al. 1999) and the distance-dependent transmission (Lima and Zollner 1996) mechanisms. However, the experiments used to demonstrate distance-dependent transmission (Lima and Zollner 1996) exclude the possibility for distance-dependent production because in those experiments only a single bird is able to detect the predator. Interestingly, the various mechanisms differ with respect to how they cause predator detection by a group of individuals to change as group radius increases (individuals are farther apart). In the case

of distance-dependent production, predators are less likely to be detected by groups of vigilant foragers when foragers are farther apart (see the appendix, section B). In contrast, for distance-dependent transmission increased distance among group members reduces the likelihood that individuals notice antipredator responses of vigilant neighbors, but the rate of detecting the predator remains constant. For the faster response mechanism, detection rates should also remain constant. Thus, we expect that it is possible to conduct experiments *in vivo* (see the appendix, section F, for a possible experiment) where the impact of distance-dependent production can be detected.

### Acknowledgments

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Illustration from “The Prong-Horn Antelope” by W. J. Hays (*American Naturalist*, 1868, 2:131–133), a response to “The Quadrupeds of Arizona” by Elliott Coues, who writes, “Over [the plains] the Prong-horned Antelope (*Antilocapra Americana*), the swiftest animal of America, runs races with the winds, making the long miles shrink into mere spans at the touch of his almost magic hoofs, whose impress upon the green sward writes down, in wild yet graceful stanzas, the ‘poetry of motion’ which every attitude and movement of his supple form embodies” (*American Naturalist*, 1867, 1:537).